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Mangroves of Arid Environments in Puerto Rico and Adjacent Islands

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ABSTRACT

The structure of mangrove vegetation, soil salinity, and topographic relief of the mangrove ecosystem were studied along the south coast of Puerto Rico, Culebra, and Mona Island. All systems, with the exception of the forest at Mona Island, were characterized by having a coastal fringe of live vegetation (usually dominated by the red mangrove), a zone of dead trees, and a hypersaline lagoon or dry salt flat on the landward side. Mean soil salinities were 44 ‰ for the zone of live trees, 72 ‰ for the zone of dead trees, and 87 ‰ for the salt flats. The Mona Island forest grew over a sandy hardpan that prevented mixing of sea water and the fresh water. Soil salinities were low in this forest, and trees reached a height of 15 m. Tree height was inversely proportional to soil salinity ($r = 0.72$) between 17 and 72 ‰. When soil salinities exceeded 65 ‰, dead tree basal area was higher than live tree basal area. It is suggested that mangrove growth is limited by soil salinities higher than 90 ‰. Mangrove succession in offshore overwash islands and arid coastlines is described. It is proposed that cyclic rainfall patterns and hurricanes act as regulators of speed and direction of succession. Rainy periods are associated with lower soil salinities and expansion of the red mangrove zone. Droughty periods result in high soil salinities, mangrove mortality, and expansion of salt flats. Hurricanes set back succession and reverse successional trends that reduce mangrove areas. A model of mangrove ecosystem function and implications for management are also discussed.

EXPANDING ON GLEASON AND COOK'S OBSERVATIONS on the mangroves of Puerto Rico (1927), Lugo and Cintrón (1975) classified Puerto Rican mangroves into two general categories: south coast and north coast types. The intensity of wave action, rainfall, and freshwater runoff were considered to be the determinant factors controlling mangrove structure and development. The environment of the south coast type forest is characterized by low rainfall (about 1000 mm), low wave energy regime, and very little freshwater runoff. Of the six mangrove forest types described by Lugo and Snedaker (1974), all but the riverine type are found on the south coast. However, the predominant type is the fringe mangrove forest. In general, south coast fringing mangroves grow by the edge of the sea, exhibit low structural complexity, low leaf fall, low rate of tree growth, and are dominated by the red mangrove (*Rhizophora mangle*). The salinity of the south coast mangroves, canals, and lagoons approaches that of sea water and varies little throughout the year. North coast type mangroves exhibit higher structural complexity and higher rates of leaf fall and tree growth. Salinities in these forests oscillate widely.

Observations of mangrove mortality associated with salt flats and/or hypersaline lagoons located landward of south coast mangroves led to this study. Similar observations were made earlier by Holdridge (1940) in Puerto Rico, Davis (1940) in south Florida, Giglioli and Thornton (1966) in West

Africa, and Macnae (1968) in western Australia. The objective of this study was to examine the conditions that contribute to the lower structural development of south coast type mangrove forests and to the mortality of trees in certain areas.

METHODS

Week-long expeditions were undertaken (in the R/V JEAN A) to the islands of Mona and Culebra off the west and east coasts of Puerto Rico (fig. 1) to study mangrove forests. Puerto Rican forests were studied at Ceiba, Salinas (near Aguirre), and La Parguera (near Ensenada), located on the island's east, south, and southwest coasts, respectively (fig. 1). All systems are found within the subtropical life zone, where potential evapotranspiration exceeds rainfall, and all were subjected to low wave energy regimes, low rainfall, and very little runoff (Ewel and Whitmore 1973, fig. 1).

At each site, a 10-m wide vegetation transect was established from the edge of the sea to the last mangrove tree landward. All trees greater than 2.5 cm diameter at breast height (dbh) were identified, and their dbh and height were measured and recorded. Diameter measurements did not include red mangrove prop roots. At some sites the point-quarter method of Cottam and Curtis (1956) was used as a substitute for the transect inventory just described. Tree heights were measured with a Haga Altimeter. In addition, seedlings were counted at 10-m increments from the shore in 1 m² plots, heights and

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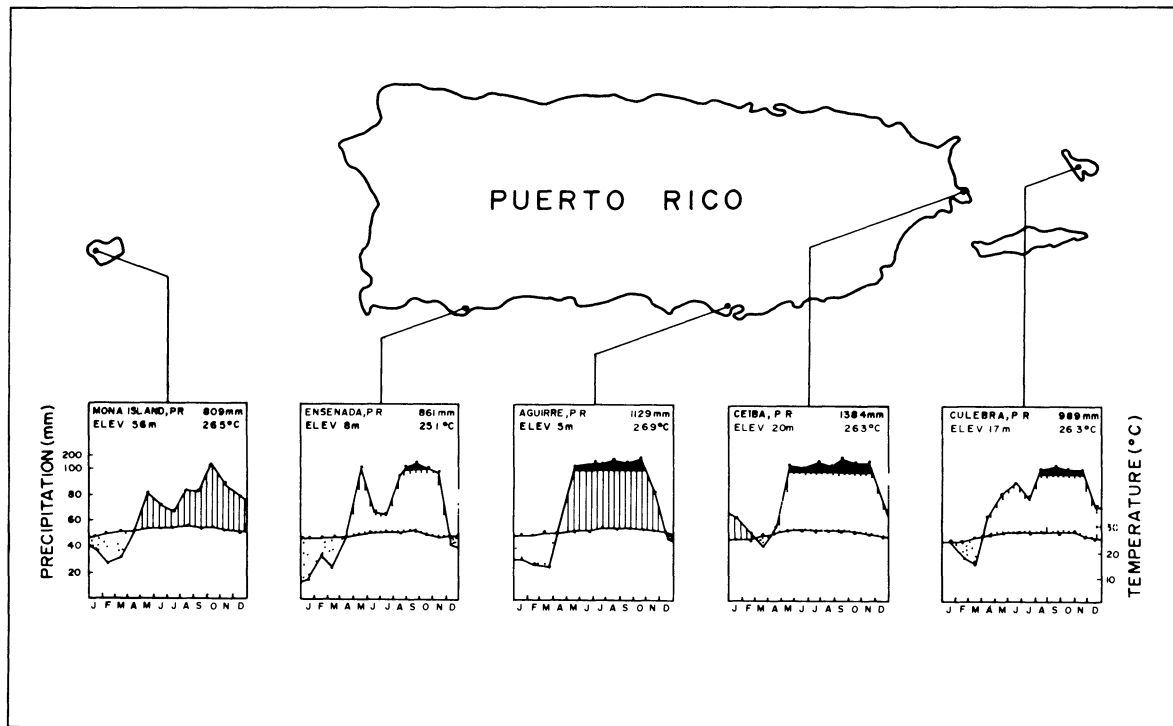


FIGURE 1. Map of Puerto Rico and adjacent islands showing the climatic regime of study sites. La Parguera and Bahía Montalva are located near Ensenada. Salinas and Las Mareas are located near Aguirre. The areas with dotted patterns below the temperature curves represent time periods when evaporation exceeds rainfall. When the rainfall curve is above the temperature curve, rainfall exceeds evaporation. Solid block represents those times when rainfall exceeds 100 mm. Mean annual temperature and rainfall are given inside each climate diagram.

densities of pneumatophores and/or lenticels were measured, and changes in species zonation noted. Soil pits were dug to observe the soil profile, to determine the level of ground water, and to measure the salinity of interstitial water (soil salinity). A portable refractometer calibrated in the laboratory against a Bisset Berman salinometer was used for salinity determinations. Surface water depth and salinity were also determined. Land levels were determined with a surveyor's transit, and the time of day was noted so that the position of maximum, minimum, and mean low water (the local tidal datum) levels would be determined from tide tables (National Oceanic and Atmospheric Administration 1975).

The past history of the vegetation in each of the study sites was reconstructed from aerial photography for 1937, 1964, 1968, and 1972, obtained from the Soil Conservation Service in Washington, D.C.

RESULTS AND DISCUSSION

CULEBRA.—Four mangrove forests were studied in Culebra. Each forest was isolated from water ex-

change with the sea to a different degree, and all four had an unvegetated salt flat behind the forest. At Zoni and at one of the two stands studied at Puerto del Manglar, there was a hypersaline lagoon instead of a dry salt flat behind the mangrove forest. Table 1 summarizes the geomorphological and structural characteristics of each site. Forests at San Ildefonso and Puerto del Manglar had no obstruction to tidal inundation, and their forest floors had a lower elevation than the forest at Zoni Lagoon. At Zoni Lagoon, a sand dune obstructed overland drainage and prevented inundation by normal tides. This forest was the one most isolated from the sea, and the forest floor was 1.38 m above mean low water (mlw). Sea water may only inundate this forest during storms, since the highest normal tides during the year only reach a height of 0.58 m. Around the Zoni Lagoon there was a 26-m-wide band of dead and dying trees. The mangrove forest was composed exclusively of the white mangrove (*Laguncularia racemosa*) and was only 20 m wide. The continuous and simultaneous enlargement of the dead mangrove zone and hypersaline lagoon could certainly result in

TABLE 1. *Structural and geomorphological characteristics of mangrove forests in Culebra, Mona Island, and La Parguera.*

Attribute	San Ildefonso	Culebra Puerto del Manglar wet dry	Zoni Lagoon	Mona Island	La Parguera Bahia Montalva Island No. 2
Height of forest floor Above mean low water (m)	0.24	0.11-0.31	0.19	1.38	0.86
Height of salt flat floor Above mean low water (m)	0.21	0.20-0.30	0.30	1.22	Absent
Maximum tidal amplitude (m)	0.58	0.58	0.58	0.58	0.91
Height of highest annual tide (m above mlw)	0.43	0.43	0.43	0.43	0.67
Height of pneumatophores (m)	0.18	—	0.18	None	None
Height of lenticels (m)	0.18	—	—	None	0.11
Height of obstruction to tidal inundation	None	None	None	2.75	2.8
Basal area of live trees (m ² /ha)	13.5	20.2	—	—	27.3
Basal area of dead trees (m ² /ha)	2.6	1.5	—	—	0

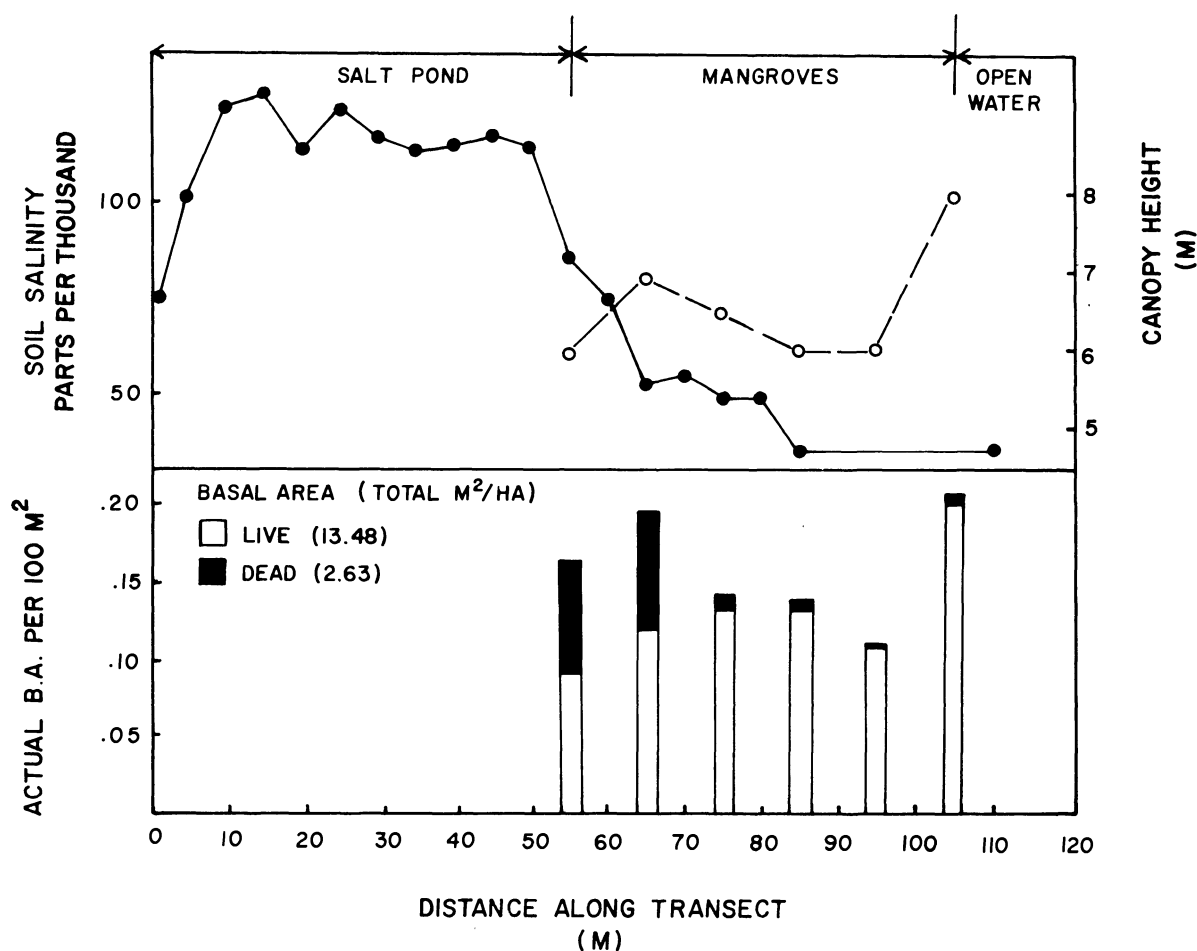


FIGURE 2. Soil salinity, vegetation height, and live and dead basal area of trees through the mangrove forest of San Ildefonso in Culebra. Solid circles represent salinity values while open circles represent canopy height.

the eventual elimination of the mangroves in that area unless the trend were reversed by some counter force. The invasion of terrestrial plants into the mangrove zone by species such as coconut palms (*Cocos nucifera*) and sea grapes (*Coccoloba uvifera*) was observed and photographed.

Changes along a transect of a typical Culebra mangrove forest are illustrated in figure 2 for the San Ildefonso forest. Similar profiles were measured at Puerto del Manglar and other sites in Puerto Rico (Bahía Montalva, in La Parguera, fig. 3, and Mar Negro, in Salinas). Three mangrove zones were evident: salt flat or hypersaline lagoon, dead-tree zone, and live-tree zone. The zone of dead trees was always found at the edge of the lagoon (fig. 2).

Table 2 summarizes soil and surface water salinity data for all study sites. Higher values for soil salinities were observed in the salt flat (means of $87 \text{ }^{\circ}/\text{00} \pm 6$ [SE]), followed by the zone of dead

trees (mean of $72 \text{ }^{\circ}/\text{00} \pm 17$ [SE]), and finally the live forest (mean of $44 \text{ }^{\circ}/\text{00} \pm 6$ [SE]). Since soil salinities are higher and vary less than surface water salinities (Lugo and Cintrón 1975), we used soil salinities for establishing correlations with species zonation, tree height, or basal area of the forest.

The distribution of seedlings and of mature trees was similar (fig. 4). Density was highest in the area where the action of waves and tides concentrated seedlings and where soil salinities were of normal seawater concentration. From that peak in density, abundance decreased to both sides of the forest. Mangroves were never found in zones with soil salinities greater than $85 \text{ }^{\circ}/\text{00}$.

MONA ISLAND.—The mangrove forest of Mona Island covered an area of 1 ha and was located 110 m inland. It was protected from tidal inundation by a sand dune that was 2.8 m high at its lowest elevation (table 1). The forest floor was elevated 0.86 m

TABLE 2. Average soil and surface water salinities in several mangrove forests of the arid coastlines in Puerto Rico and adjacent islands. (Values are in $^{\circ}/\text{00}$ (1 SE).)

Site and date	Salt Flat or Lagoon		Zone of dead trees		Live forest	
	Soil	Surface	Soil	Surface	Soil	Surface
Culebra						
San Ildefonso						
August, 1974	—	37.0	—	—	—	—
May, 1975	114 (25)	—	80 (4)	—	—	—
June, 1975	112 (6)	96 (1)	114 (2)	—	61 (5)	—
Puerto del Manglar (wet)						
June, 1975	67 (2)	56 (.5)	—	—	46 (3)	—
Puerto del Manglar (dry)						
June, 1975	76	—	—	—	49 (5)	—
Zoni Lagoon						
August, 1973	—	62	—	—	—	—
June, 1974	37 (5)	24 (.5) 27 (1.5) ^a 67 (.7)	34 (5.8)	25 (1)	21 (5)	—
July, 1974	—	—	—	—	19	—
Flamenco Lagoon						
August, 1973	—	73	—	—	—	—
May 15, 1973	—	287	—	—	—	—
May 22, 1973	—	75	—	—	—	—
June, 1975	—	101	—	—	—	—
Mean for Culebra	87 (18)	82 (22)	76 (23)	25 (1)	39 (8)	—
South Coast of P.R.						
Mar Negro, Salinas						
August, 1975	—	69	61	—	50 (3)	37
Mona Island						
July, 1975	Absent ^b	Absent	Absent	Absent	17 (7)	—
Bahía Montalva, La Parguera						
Island No. 1						
April, 1967	—	175 (2)	—	—	56 (5)	41 (3)
Island No. 2						
August, 1975	—	53 (.4)	—	—	66 (4)	42 (4)
Ceiba, Puerto Rico						
Roosevelt Roads						
April-August, 1975	Absent	Absent	Heavy mortality throughout		59 (1)	—
Mean of all determinations	87 (18)	86 (18)	72 (17)	25 (1)	44 (6)	40 (2)

^a Bottom samples.

^b Means that the mangrove zone was not present in this location.

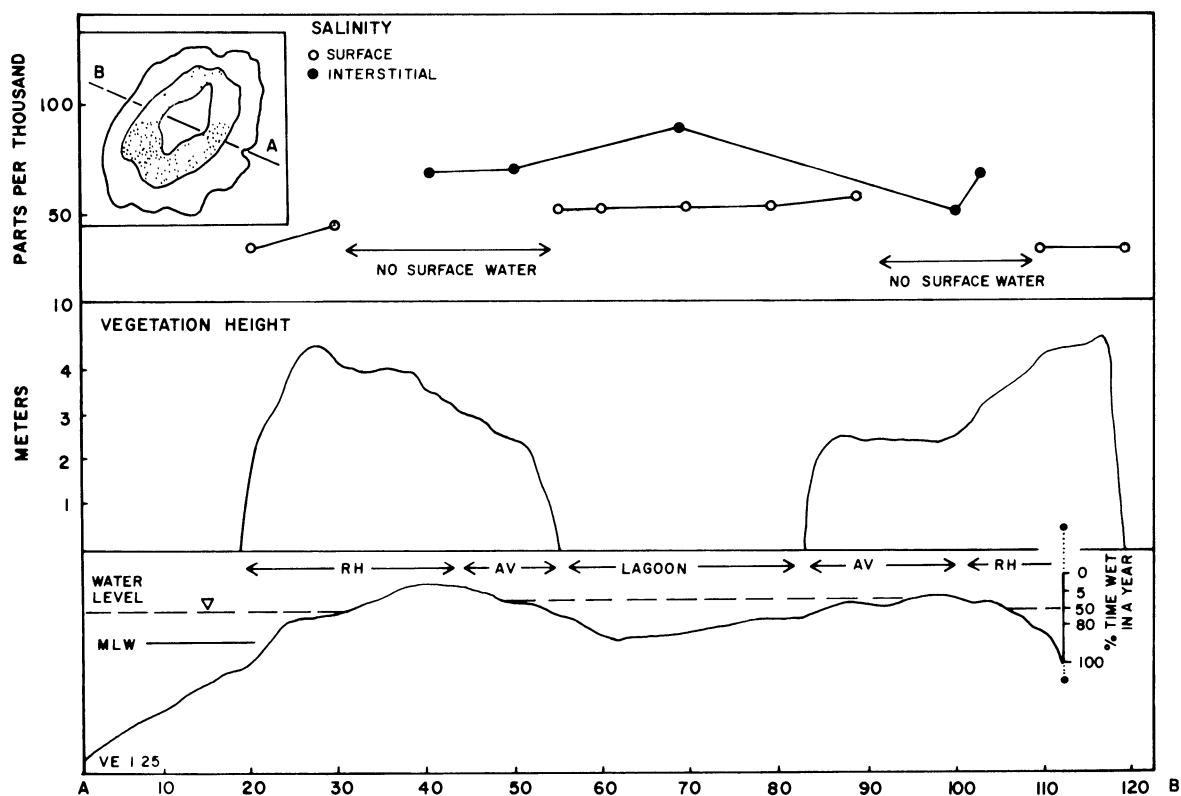


FIGURE 3. Interstitial and surface water salinity, vegetation height, and topographic relief variation through a mangrove island located in Bahía Montalva, La Parguera. The percentage time that the water level remains at a given elevation plus the extreme water levels reported for this locality (two solid dots connected by dotted lines), are shown in the lower right side of the figure. RH is *Rhizophora mangle*, and AV is *Avicennia germinans*.

above mlw and beyond the reach of the highest annual tides (storms not included). This forest was dominated by red mangroves with a basal area of 27.3 m²/ha, a mean canopy height of 13 m, and unusually large leaves (length of 11-15 cm and width of 5-6 cm). Scattered white mangroves were growing on the landward edge of the forest, at the ecotone with a subtropical dry forest that was located between the mangroves and a limestone wall about 50 m high.

Soil water salinities at Mona Island were the lowest of all the forests studied (table 2). Salinities (in ‰) from soil pits dug every 10 m starting at the seaward edge of the forest were: 21.6, 27.4, 34.9, 1.7, and 0 (the fourth and fifth pits were 20 m apart). While digging the pits, we observed a sandy hardpan (about 10 cm thick) running underneath the forest at a mean soil depth of 32 cm. The soil was dry above the hardpan, and mangrove roots reached the water table by penetrating the hardpan. This hardpan may prevent sea water seeping in from

the sea from mixing with fresh water that percolates from the island's plateau and down the steep cliffs behind the forest. Thus, the Mona Island mangrove forest, although located in an arid environment, is standing over a pool of low-salinity water that supports its rapid and extensive growth and development. A breach in the protective dune suggested periodic overtopping by large storm waves. This opening was 6 m wide and about 2.8 m above mlw. Personnel on the island recalled at least two instances in which overtopping and consequent flooding of the area behind the dune had occurred: in 1967 and in the early 1970s. When this flooding occurs, salt water is trapped above the hardpan and may contribute to the maintenance of higher soil salinity in those forest areas located nearer the sea.

LA PARGUERA.—Fringe mangroves predominate along the coastline near La Parguera. Offshore overwash islands of red mangroves develop over shallow plat-

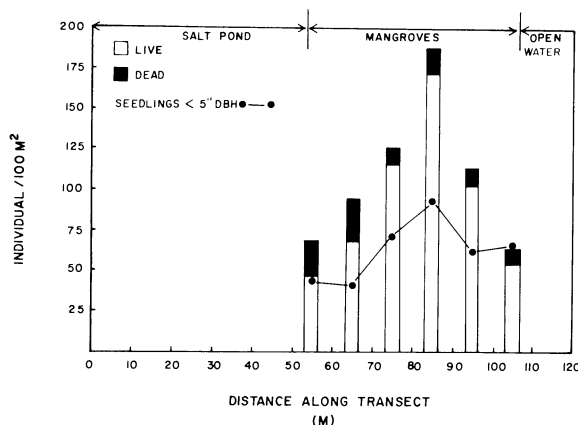


FIGURE 4. Density of live and dead stems and seedlings through the mangrove forest of Puerto del Manglar, Culebra.

forms. Many of these islands are overtopped daily by high tides. Others are overtopped less frequently, and only the highest tides flush through their whole length. The difference is due to two factors: 1) slight elevation differences amongst islands; and 2) the role of dense growth of red mangrove prop roots and of the shallow seaward shelf that protects these islands from wave action (fig. 3).

Fifty transects were measured on a 1968 aerial photo to determine the width of the fringe forest on the windward and leeward sides of each of these mangrove islands. Figure 5 shows that the fringe areas were 3.5 times wider toward the windward than to the leeward side. This may be due to a greater wave energy regime on the windward face, which could reduce the rate of accumulation of materials at the edge. This reduction might also enhance the flow of water toward the interior of the island. The contact with fresh sea water over a greater distance inland would allow a wider and more vigorous red mangrove fringe to develop. However, as wave energy is dissipated by the prop root maze, the rate of sedimentation of detrital material would increase. A gentle slope would form inland and result in a decrease in the frequency of tidal flushing. The decrease in tidal flushing coupled with the aridity and high evaporation of the region could in turn contribute to the development of higher soil salinity conditions and favor further accumulation of plant detrital material (fig. 3, table 2). The lower wave activity in the leeward side of the island thus probably accounts for the narrower fringe of red mangrove forest.

SUCCESSION ON SMALL MANGROVE ISLANDS

The succession of mangrove species on the shallow bank or offshore platform begins with scrub red

mangroves growing as isolated individuals over *Thalassia* beds. Margalef (1962) and Welch (1962) described this succession, which begins from submerged bare marine sands and may pass through a coral reef stage. Undoubtedly, this colonization by red mangroves is very slow and could lead to the development of a mangrove overwash island. In these islands mangrove growth is favored by soil salinities of 35 ‰ or less and by the continuous low-intensity flushing of waves and tides. Casual field observations suggest that wave intensity may enhance the development of prop roots. The vigor of mangrove growth will also depend upon the nutrient richness of soil water and is probably accelerated by the activity of bird rookeries (Valiela and Teal, pers. comm.). As topography and soil salinity change inside the island (as discussed above), red mangroves are replaced by the more salt-tolerant black mangrove (*Avicennia germinans*). If soil salinities remain high but stable, large and vigorous trees of this species may become established in the core, surrounded by a ring of red mangroves (fig. 6). If the salinity continues to rise, the growth of black mangrove is stunted. The island then assumes an "annular" appearance with a ring of red mangroves around an inner core of stunted black mangroves (fig. 3). Eventually, conditions may become so restrictive that the core is left devoid of trees. As trees die, a shallow depression (10-20 cm deep) is formed (fig. 7). This lagoon is colonized

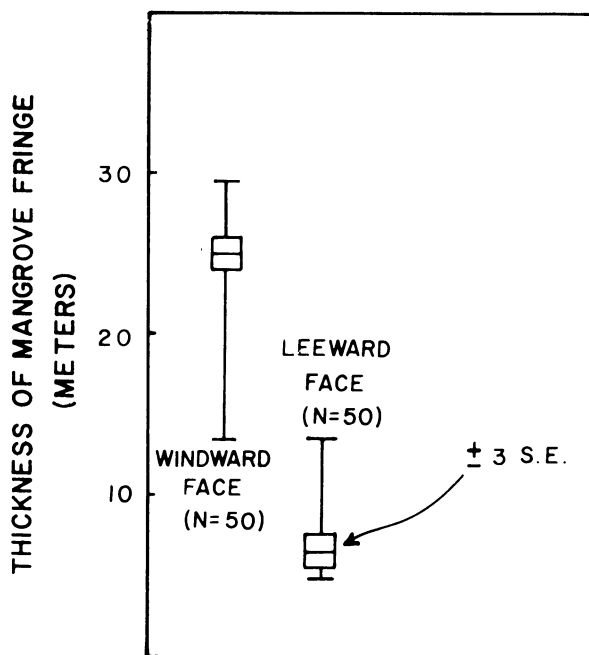


FIGURE 5. Thickness of the red mangrove fringe in the mangrove islands of La Parguera.

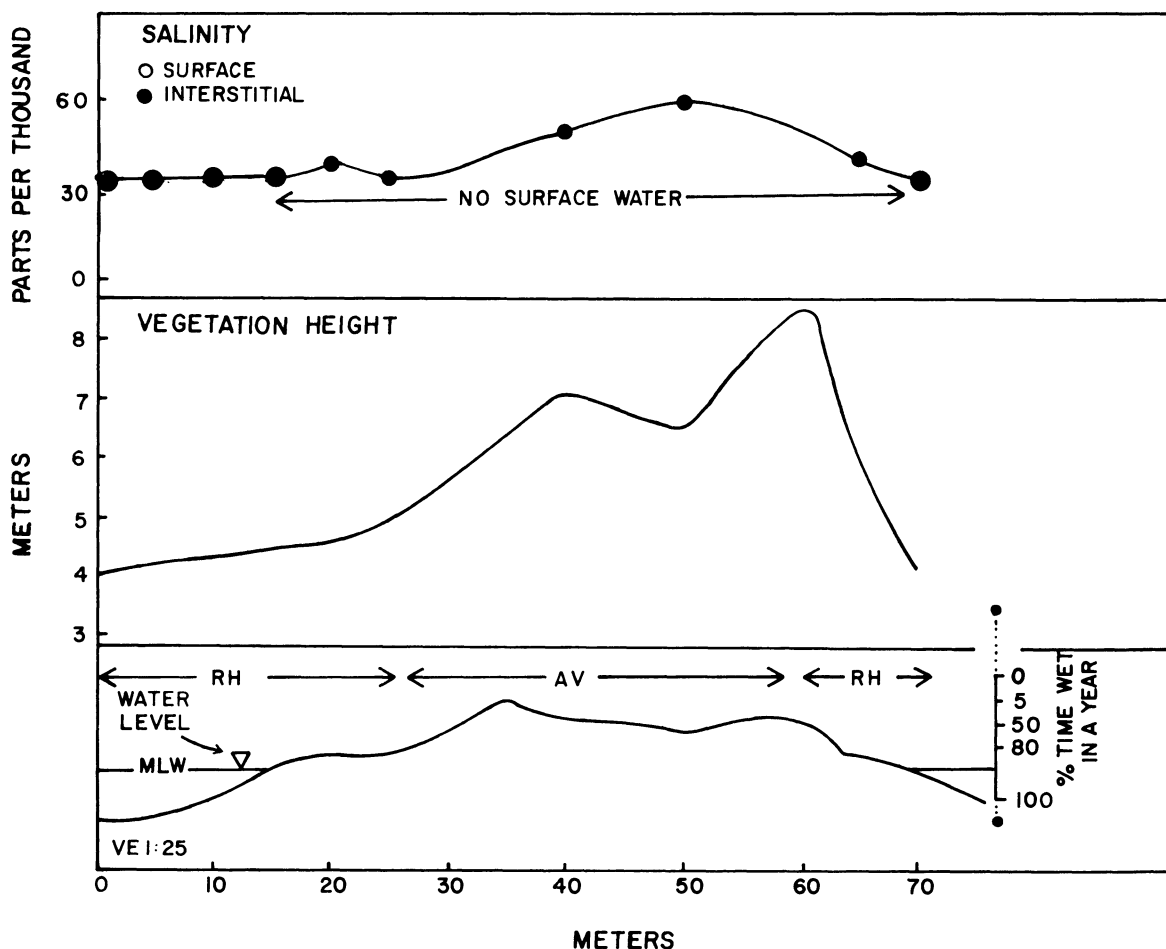


FIGURE 6. Interstitial and surface water salinity, vegetation height, and topographic relief through a mangrove island (at La Parguera) with a core of tall and vigorous black mangrove trees. Surface water salinity on the first 15 m of the transect had the same value as interstitial waters. The percentage time that the water level remains at a given elevation and the extreme water levels reported for that location (two solid dots connected by dotted line) are shown in the lower right side of the figure. RH is *Rhizophora mangle*, and AV is *Avicennia germinans*.

by mats of blue-green algae. Water temperatures in the lagoon are of the order of 30-40° C, and waters may be rust-colored from the presence of halophytic bacteria. The high water temperatures may affect tree growth, and probably cause considerable root mortality. As roots die and collapse, the lagoon may increase in depth.

Figure 8 illustrates the events leading to the formation and destruction of mangrove islands in an arid coastal zone. Hurricanes or storm flushing seem to be the only natural mechanisms capable of reversing the development of hypersaline soil conditions. Most succession schemes for mangrove forests suggest the inevitability of a terrestrial climax (Gleason and Cook 1927, Davis 1940, Welch 1962). However, these schemes ignore the reversals caused by hurri-

canes and other destructive forces. Stoddart (1962) described the reversal of mangrove succession to an earlier stage in British Honduras as a result of hurricane Hattie. However, he implied that the leveling of mangrove islands requires the direct impact of the storm. Different islands, depending on their size and degree of disturbance by man (cutting, alteration of drainage, etc.) or natural forces, may be set back to any of the stages shown in figure 8. A return to the primary stage of succession is a low-probability event, influenced by the storm's strength and proximity to the island.

SUCCESSION OF MANGROVES ON ARID COASTLINES

Fringing mangroves undergo successional develop-

ment similar to that suggested for small islands. Vigorous plant growth at the water edge results in a restriction of water circulation to the inner parts of the swamp. Given time, drainage canals become clogged by detritus and invaded by mangroves. Soil

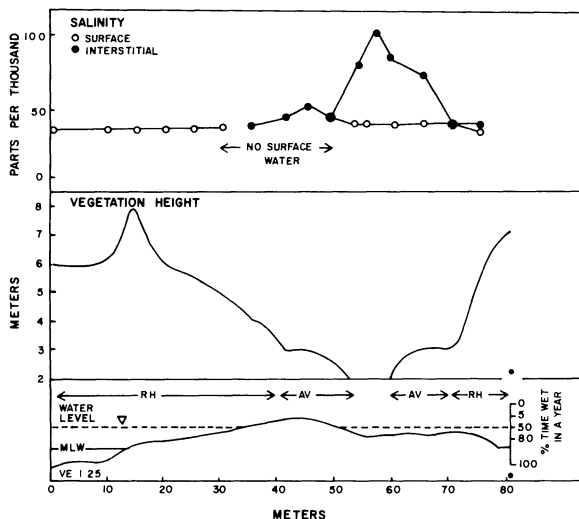


FIGURE 7. Interstitial and surface water salinity, vegetation height, and topographic relief through a mangrove island (at La Parguera) with a core of dwarf black mangroves and a hypersaline lagoon. The percentage time that the water level remains at a given elevation and the extreme water levels reported for that locality (two solid dots connected by dotted line) are shown in the lower right side of the figure. RH is *Rhizophora mangle* and AV is *Avicennia germinans*.

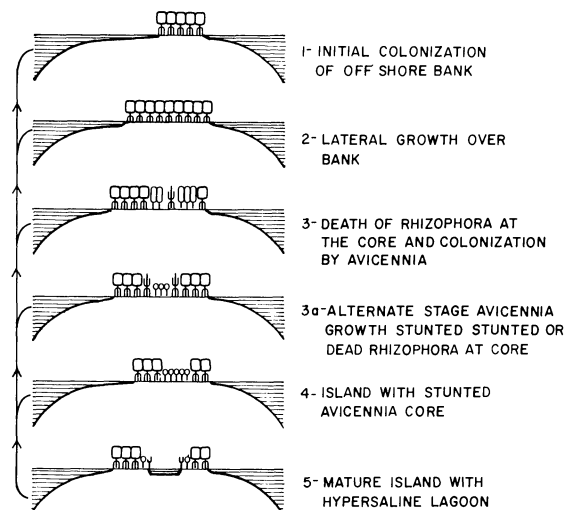


FIGURE 8. Conceptual scheme of mangrove succession for mangrove islands in arid coastlines. Note that natural or human-induced forces may set back succession to any stage. The degree of the setback depends on the intensity of the force.

salinities in the inner parts of the swamp would then increase, and these areas may be invaded by the more salt-tolerant black mangrove. Eventually, extensive areas of the inner swamp may die, resulting in the formation of salt flats. Again, we propose that storms could delay or rejuvenate the sequence. Strong winds and wave action from severe storms could destroy the mangrove fringes and bring large water flows that would unclog or open new drainage canals into the forest. Through these openings, sea water could intrude and create favorable conditions for invasion by red mangroves. Signs of clogging of natural canals and die-offs in the inner parts of the swamp are common along the south coast of Puerto Rico (e.g., Las Mareas, near Aguirre). Here, in the middle of the hypersaline lagoons, we found the remains of dead red mangroves trees, and in many instances dead barnacles were found attached to the dead roots. This finding is evidence that the circulation in these areas was once great enough to allow the growth of these animals on mangrove roots.

Mangrove succession on the mainland may be complicated by sediments from the land (where there is enough runoff), or from the sea (when storms bring in excessive sand). When this happens, succession may advance rapidly to terrestrial systems, as in Zoni Lagoon. Severe hurricanes may be capable of reversing this trend (see below).

SOIL SALINITY AND MANGROVE ECOSYSTEM STRUCTURE

Figure 9 shows the relationship between height of mangrove trees and soil salinity. Smaller mangroves are associated with higher soil salinities. Figure 10 suggests a rapid increase in mangrove tree mortality beyond a soil salinity threshold of about 65 ‰. Red mangrove tree density changes along a soil salinity gradient are illustrated in figure 11. These data and field observations suggest that in a large region with similar patterns of high air temperature, low rainfall, and very little terrestrial runoff (as the arid south coast of Puerto Rico), mangrove growth responds to soil salinity variations and is eventually restricted by high soil salinities.

The limits of mangrove growth with respect to soil salinity appear to be at 2.5 times (about 90 ‰, the concentration of salt in normal sea water). Scholander *et al.* (1965) found sap pressures of mangroves high enough to extract fresh water from water with a salt concentration about 2.5 times normal sea water. In his description of salt flats in western Australia, Macnae (1968) observed species changes and increasing scrubbyness with increasing soil sa-

linities. He reported dwarfed *Avicennia marina* growing at a soil salinity of 90 ‰. Adams (1963) found a limit of 70 ‰ for the establishment of salt marshes in North Carolina. Davis (1940) reported scrub black mangroves at a maximum of 80 ‰ in south Florida. Giglioli and King (1967) measured soil salinities as high as 82 ‰ in Keneba. *Avicennia germinans* was only found in salinities up to 58 ‰. In no report were mangroves found to be growing at soil salinities greater than 90 ‰.

Based on our observations and findings of a de-

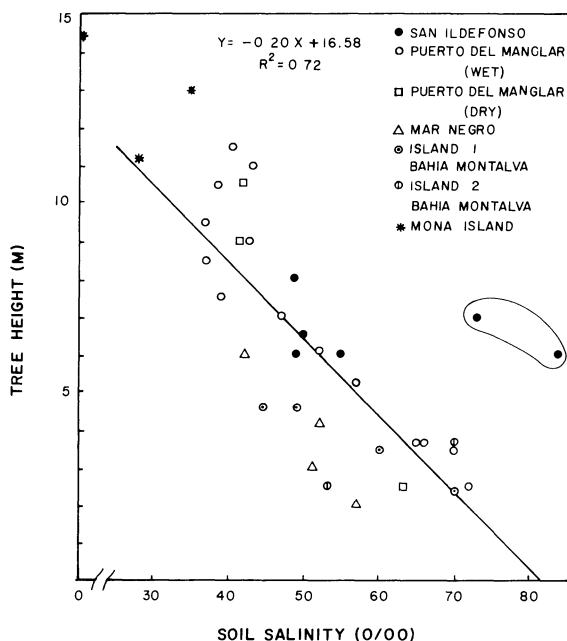


FIGURE 9. Relationship between tree height and soil salinity in mangroves of arid coastlines of Puerto Rico and adjacent islands. The two encircled data points were excluded from the regression.

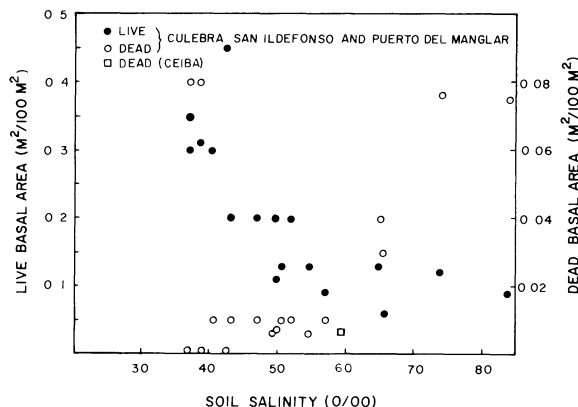


FIGURE 10. Live and dead basal area of trees along a soil salinity gradient in the mangroves of Culebra and Ceiba, Puerto Rico.

crease in transpiration and net productivity, plus an increase in respiration with increasing soil salinity (Carter *et al.* 1973, Burns 1975, Hicks and Burns 1975, Lugo *et al.* 1975), we propose a model to summarize how various factors may affect mangrove growth, structure, and metabolism (fig. 12). In the model, flushing by tides or riverine flows, plus nutrient inputs, are factors which accelerate mangrove growth and augment structural development. However, high soil salinity imposes an energy "cost." This cost must be met from energy reserves if fresh water is to become available to maintain the internal salt balance, cell turgor, the transpiration stream, and the openings of stomata for gas exchange. When the transpiration stream is active, nutrient concentration in the photosynthesizing leaves is possible, and gas exchange and productivity are high. As soil salinity increases, the cost of obtaining fresh water increases. This condition causes a higher respiratory cost, lowers the net productivity, and decreases the ability of trees to concentrate nutrients in photosynthesizing leaves. If this condition is prolonged, changes in both species and structural composition must occur. These changes might lead to shorter forests where root pressures may be sufficient to transport the nutrients to the leaves, or where low rates of transpiration support very low rates of productivity (Lugo and Snedaker 1974). The increased energy costs associated with adaptations to high soil salinities have recently been discussed by Waisel (1972), Queen (1974), and by Poljakoff-Mayber and Gale (1975).

CYCLIC CHANGES OF MANGROVE STRUCTURE

Mangroves have sometimes been portrayed as land builders that continuously gain land from the sea.

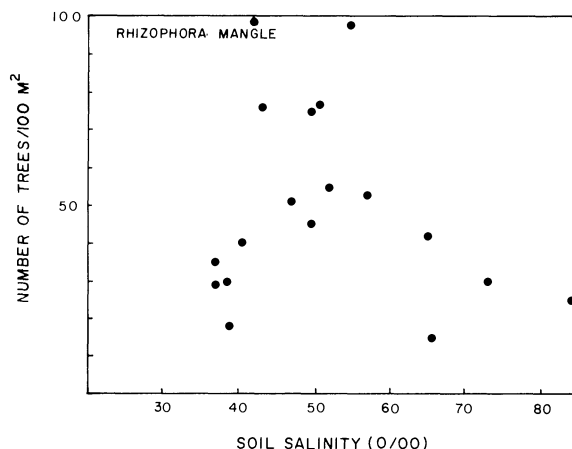


FIGURE 11. Density of red mangroves along a soil salinity gradient in the mangroves of Culebra.

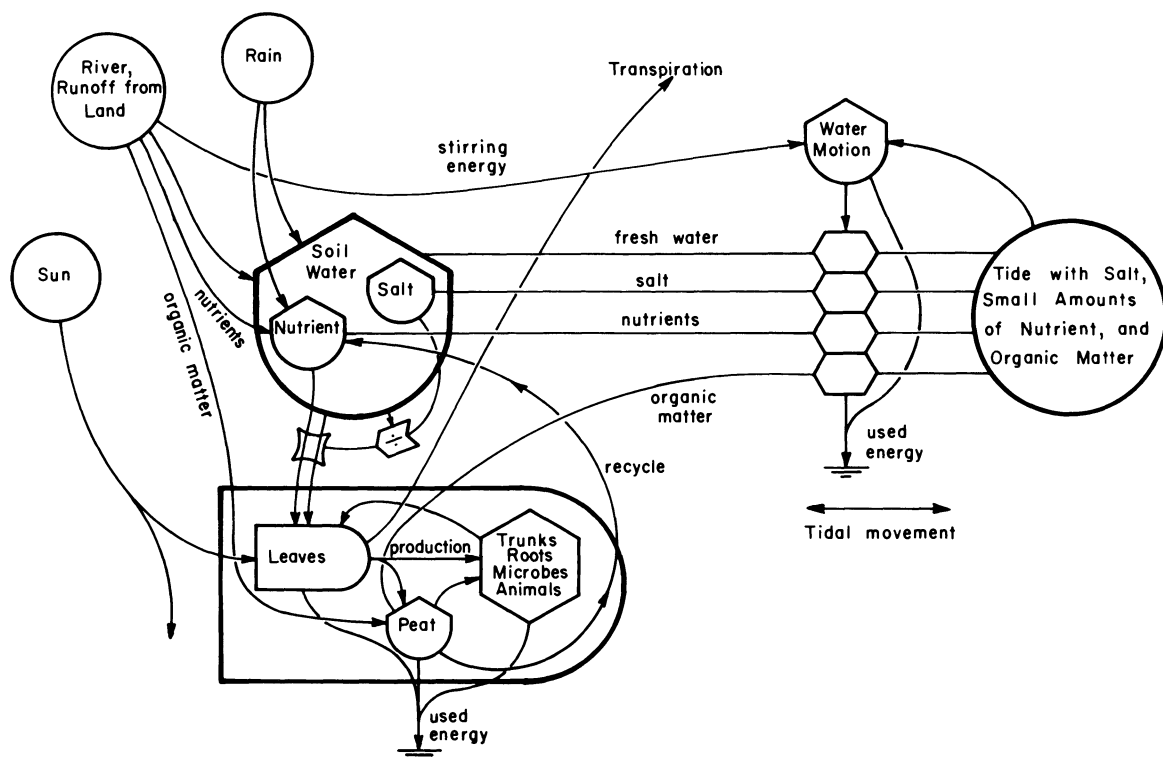


FIGURE 12. Energy flow model of mangrove ecosystems. Symbols are from Odum (1971). The model depicts biomass accumulations; the processes of productivity, respiration and cycling; input and output of nutrients (net input) and organic matter (net output); and the factors (both internal and external) believed to control these rates.

However, Thom (1967) and Lugo and Snedaker (1974) have discussed situations where mangroves do not necessarily gain land from the sea, but where they may actually lose it. Analysis of aerial photos, measurements of elevation, and observations of the effects of soil salinity on mangrove structure indicate that mangrove areas in arid environments fluctuate between periods when they decrease in size (and, therefore, lose ground to the sea or to terrestrial systems) and periods of expansion. For example, we found that the mangrove forest bordering the Zoni Lagoon in Culebra (now only 20 m wide) expands in size after hurricanes destroy its protective dune. Inundation of the hypersaline lagoon area by fresh sea water and rain follows. As a result, soil salinities apparently decrease, allowing an invasion of red mangroves and expansion of the forest. These areas then become productive fisheries (pers. comm. of many local fishermen). Similar expansions were documented from aerial photos for sites at Ceiba and Ensenada Honda. However, during periods between hurricanes the mangrove forests slowly decrease in size, presumably due to the effects of increasing

soil salinity. Terrestrial systems may invade mangrove areas where hurricanes or storms have deposited high sediment loads that increase the elevation of the mangrove forest (e.g., Zoni Lagoon).

Cyclic patterns in rainfall may also affect mangrove growth and regeneration, even in the absence of hurricanes. Reports of cyclic rainfall phenomena are given by Bowden *et al.* (1970) for the U.S. Virgin Islands and for Florida by Moran (1975). In areas where overland runoff is insufficient to neutralize the effects of decreased rainfall, dry periods may be characterized by dying back or reduction of mangrove areas, followed by expansion as rainfall increases. Recent observations in the mangroves of south Florida suggest the presence of the same train of events. For example, Davis and Hilsenbeck (1974) documented increases of salinity in the Shark River Estuary from 10-23 ‰ between 1955-1962 (wet years), to 19-42 ‰ between 1962-1974 (drier conditions). These increases were coupled with mangrove mortality, reduction in the crocodile populations, death of sawgrass, and shifting in the feeding areas for wading birds. While there were changes

in the amount of overland runoff to their study area, they also reported decreases in rainfall between the two time periods.

IMPLICATIONS

The cyclic mortality and expansion of mangrove forests in response to cyclic climatic events appears to be a common feature of arid coastlines. The climatic cycles may be associated with hurricanes (periods of 10-30 years) or with rainfall (periods of 5-10 years). This association has at least two implications for mangrove management. First, managers should consider open water areas and salt flats part of the mangrove ecosystem and not as separate eco-

systems. Failure to recognize this fact may result in incompatible land uses that may affect the normal expansion of the mangrove forest during periods of high rainfall and lower soil salinities. Secondly, periods of high mangrove mortality are normal occurrences in these environments, and care should be taken before attributing this mortality to other factors, including man and isopods.

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NOTE

A Bat-Generated Fig Seed Shadow in Rainforest

On 24 November 1977, in the primary rainforest above the Rio Cameronal, Sirena, Corcovado National Park, Osa Peninsula, Costa Rica, I encountered an area of understory vegetation liberally sprinkled with bat fecal splats containing only fig seeds of one size. On the vegetation, nearest neighbor distances between splats was about 1 meter, but as leaves covered only about a tenth of the ground, I suspect that they occurred at a density of about 10 per m² over an area of at least 2500 m². The seeds were counted in 119 splats and had the following distribution of seeds, beginning with 1 per splat: 0, 2, 5, 3, 6, 5, 6, 5, 3, 7, 4, 8, 9, 3, 7, 6, 4, 7, 3, 5, 1, 1, 3, 1, 2, 1, 1, 1, 2, 1, plus 1 each with 34, 35, 38, 39, 41, 42, and 43 seeds ($n=119$, $\bar{X}=14.7$, $s.d.=8.9$ seeds per splat). This result means that the bats had deposited about 367,500 fig seeds in a small area. One aroid leaf about 0.25 m² in area had 17 splats with a total of 242 seeds, but they were particularly concentrated on the foliage in its general vicinity.

I identified the fecal splats as belonging to bats because there were so many, because there were no other materials in them than the seeds of one species of fig, and because there was no trace of white urates associated with any splat. While figs customarily contain 30 to 60 percent seeds with fig wasp exits, it was most striking that all the seeds in the splats were intact seeds. This finding strongly suggests that the bats either thoroughly digest all parts of the fig other than the intact seeds, or are very selective in eating only the wall of the fig syconium and the immediately adjacent (usually) intact seeds (those with wasp exit holes tend to be more in the center of the fig).

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